1988

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Recommended Citation

Jurik, T. W.; Briggs, G. M.; Gates, D. M. 1989. Aboveground biomass and production from 1938 to 1984 for four aspen plots in northern lower Michigan. Mich. Bot. 27 (2): 43-54.

ABOVEGROUND BIOMASS AND PRODUCTION FROM 1938 TO 1984 FOR FOUR ASPEN PLOTS IN NORTHERN LOWER MICHIGAN

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The University of Michigan Biological Station has several permanent study plots established in 1938 on which growth of individual trees has been monitored. These permanent plots provide a rare opportunity for determining changes in biomass and species composition during successional forest regrowth after cutting and burning, in that a true temporal sequence of samples on a single site is available. Such temporal sequences spanning more than one or two decades are extremely uncommon (Peet 1981). As a result, most studies of successional forest regrowth have necessarily assumed that a spatial array of different-age stands studied at one point in time represents the temporal sequence occurring on any one site, even though the validity of that assumption is not known.

Our primary objective here was to provide data on forest stand biomass and production that could be used to test hypotheses concerning forest growth after disturbance; the data also revealed successional trends in species importances on the plots. Our calculations of standing crop and production, via use of allometric equations, included the effects of mortality and recruitment on the plots. In contrast, most other studies of biomass and production have either neglected the turnover of stems or had to estimate turnover rates, thus introducing more uncertainty into the calculation. We demonstrate that the effects of uncertainty in time of mortality and recruitment of stems between sample dates are small.

HISTORICAL BACKGROUND AND FIELD SITES

The field sites are located at the University of Michigan Biological Station near Pellston, Michigan, U.S.A. (45°33'N, 84°42'W). Soil parent

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materials of this region are primarily of glacial origin. Soil texture is particularly variable, a characteristic that has had substantial impact on the vegetation occupying individual sites. Heavier-textured soils, mostly loams, derived from glacial till supported pre-settlement forests dominated by northern hardwoods (Gates 1930). Sandy soils derived from glacial outwash plains supported pre-settlement forests dominated by red pine (*Pinus resinosa*), eastern white pine (*P. strobus*), and eastern hemlock (*Tsuga canadensis*) (Gates 1930, Kilburn 1960a,b). Nomenclature follows Barnes and Wagner (1981). During the late 19th and early 20th centuries the entire area was logged. Regrowth after logging was hampered by frequent fires early in the 20th century (Kilburn 1960b). The combination of logging and fires drastically altered the composition and size of the forests in the area. Hemlock all but disappeared, and both pine species were reduced in importance. Bigtooth aspen (*Populus grandidentata*) and trembling aspen (*P. tremuloides*) became dominant species in much of the region (Kilburn 1960b). Many of the areas with heavier-textured soils have remained in agricultural use.

In 1938, F. C. Gates and W. F. Ramsdell set up seven 0.1 acre (0.04 hectare) plots that exhibited the range of forest and soil types found in or near the Biological Station, with the intention that forest development on the plots be traced for at least 50 years. One of the seven plots was logged soon after establishment and was not studied thereafter. Two plots on organic wetland soils are discussed in Sakai and Sulak (1985). The four plots dominated by aspen are analyzed here. Successional history of the plots was discussed by Roberts and Richardson (1985). Wells (1978) and Sakai et al. (1985) studied changes in stand composition in another plot comparable to our plot 4. Detailed descriptions of the sites are given by Roberts and Richardson (1985); we give brief summaries below.

Plot 2 is on a well-drained, flat area of sandy glacial outwash. The soil is a sandy, mixed, frigid, Entic Haplorthod (unpublished U.S.D.A.-S.C.S. map, 1976; Grayling, Michigan). Plot 3 occurs on a "sandy, somewhat stoney, glacial moraine with a small slope to the northwest" (Sylvester 1939, unpublished University of Michigan Biological Station student paper). The soil is a sandy, mixed, frigid, Alfic Haplorthod. Plot 4 has a mixed, frigid, Alfic Haplorthod soil with a surface layer of sand underlain by a layer of sandy clay at a depth of one meter; the site has a 10% slope to the northeast. The presence of clay improves both the water and nutrient retention properties of the soil (Hannah & Zahner 1970, Adams & Boyle 1982) and is reflected in better tree growth. Plot 5 is located in a flat area with sandy soils only one to two m above the water table of Douglas Lake. The soil is a sandy, mixed, frigid, Ortstein aeric Haplaquad.

As judged from increment cores, the oldest trees on Plot 2 appeared about 1909, presumably following one of the fires that swept the region. The oldest trees on Plots 3, 4, and 5 date from about 1919. It is unknown whether the oldest trees are of sprout or seedling origin.

METHODS

Each tree ≥ 1.0 m tall on a plot was identified, mapped, and its DBH (diameter at breast height, 1.4 m above ground) measured in the years 1938, 1945, 1951, 1955, 1968, 1973, and 1979. Plot 5 was not studied in 1968. This procedure produced data on the histories of individual stems, thus allowing determination of mortality and recruitment. In 1984, trees on all four plots were identified by species and measured but not mapped, so that the histories of individual stems between 1979 and 1984 were not known.

On each of the plots, estimates were made of aboveground standing crop (hereafter referred to as standing crop) and aboveground production (hereafter referred to as production) by use of allometric equations based on tree DBH. For each of the plots, we estimated standing crop from 1938 to 1984 using the equations of Cooper (1981), which were based on samples from the Biological Station, except for white pine and red pine. Cooper combined data for large white pine from North Carolina and large red pine from Minnesota with data for smaller trees from the Biological Station, to produce equations for those two species. Cooper developed equations for prediction of standing crop of leaves, live branches, dead branches, and boles for ten species, including all of the dominant trees in the area and most of the subdominant species, except sugar maple (*Acer saccharum*). Here, equations for red maple (*A. rubrum*) were used for sugar maple, which was a minor component of the forests. Equations for shadbush (*Amelanchier* sp.) were used for several understory species that Cooper did not study. We used our own equations (Briggs et al., in preparation) for aspen stems less than 5 cm diameter and Cooper's equations for larger aspens. The degree of error involved in applying these equations to stands of different ages is unknown. Cooper's equations are based on trees from sites of poor quality, similar to our plots 2, 3, and 5. We used the same equations for all our sites, even though Koerper and Richardson (1980) used different equations for aspen on poor versus moderate and good sites at the Biological Station, because Cooper's equations were based on a broader range of stand ages. Koerper and Richardson's (1980) results suggest that our values for standing crop and production for aspen on the good site (Plot 4) may be underestimates.

For each of the sample years, we used existing records of DBH for each individual tree. Stem diameter was interpolated for years between the sample dates using the assumption that the rate of diameter growth was constant over the sample interval, i.e., the average rate of diameter growth for an interval was calculated from the total diameter increment divided by the total time a tree was alive in an interval. For trees dying in an interval, we assumed no diameter growth occurred between the preceding sample date and the year of death; we assumed trees appearing (i.e., that became taller than 1.0 m and were first counted) in an interval grew a maximum of 1 cm in diameter per year. Since trees were not mapped in 1984 (so that individual stems from previous samples were not distinguished), DBH was not estimated for the years 1980–1983.

We determined upper and lower limits for standing crop and production for dates between the sample years by making different assumptions about when trees died or appeared. A lower limit was produced by assuming that all trees dying in the interval between two sample years died in the first year following the first sample date and all trees appearing in the interval appeared at the end of the interval. An upper limit was produced by assuming that all trees dying in the interval died immediately before the end of the interval and all trees appearing in the interval appeared at the start of the interval.

Production on each plot was calculated for each year from 1939 through 1979. Production of bole material, live branches, and dead branches was calculated from the difference in standing crop values of each tree on successive years. Leaf and small twig production for each living tree on the plot was taken to be the standing crop biomass of leaves and small twigs estimated as described above, except for evergreen species, where leaf production was assumed to be 0.3 of the standing crop (Cooper 1981).

Data on recruitment, mortality, and density of stems on the plots are given by Roberts and Richardson (1985). Our calculations are based on the same historical records used by them and so can be related directly to their results. Briefly, aspen is being replaced in the canopy by red pine, white pine, red maple, and red oak, with sugar maple and beech increasing in abundance

TABLE 1: Total stem densities (#/ha), by size class (cm), for the plots.

Year	0-1	2-6	7-11	12-16	17-21	22-26	27-up
Plot 2							
1938	890	1483	815	173	0	0	0
1945	445	1235	618	420	0	0	0
1951	692	1384	642	445	124	0	0
1955	766	1137	544	420	222	0	0
1968	346	964	346	469	247	124	0
1973	74	1063	395	371	272	198	25
1979	173	815	346	297	346	198	25
Plot 3							
1938	2001	3533	198	99	74	0	0
1945	2150	2767	371	99	49	49	0
1951	1927	1878	791	99	74	25	49
1955	1581	1334	939	222	49	49	49
1968	1606	1384	642	420	74	49	99
1973	766	1656	568	469	124	49	99
1979	2767	1408	593	321	272	0	148
Plot 4							
1938	3385	6350	1186	148	25	0	0
1945	914	4472	1829	494	25	0	0
1951	395	2718	1013	791	272	25	0
1955	469	1754	865	642	371	49	25
1968	2718	939	840	272	494	247	99
1973	2545	2174	815	198	445	297	148
1979	3039	1532	741	99	321	198	247
Plot 5							
1938	1310	1334	1161	124	0	25	0
1945	3385	642	321	99	0	0	0
1951	1680	1137	297	74	49	0	0
1955	1557	717	346	74	25	25	0
1973	198	791	297	49	197	25	25
1979	618	568	247	49	173	74	0

in the understory. These trends in species replacements are also indicated in Table 2. Patterns of recruitment and mortality will not be addressed further here.

RESULTS

Total stem densities in the smaller size classes generally decreased from 1938 to 1979, while density in larger size classes increased (Table 1). The increase in number of larger stems led to an increase in total aboveground standing crop of trees on each of the plots over the period 1938–1984 (Fig. 1). In 1938, the standing crop ranged from 1.8 kg/m^2 on plot 3 to 3.7 kg/m^2 on plot 4, which had the highest-fertility soil. Although the forest on plot 2 was about 29 years old in 1938, as compared to 19 years for forests on the other three plots, plot 2 had the second lowest total standing crop in 1938. Standing crop on plot 5 decreased precipitously from 1938 to 1945 (see

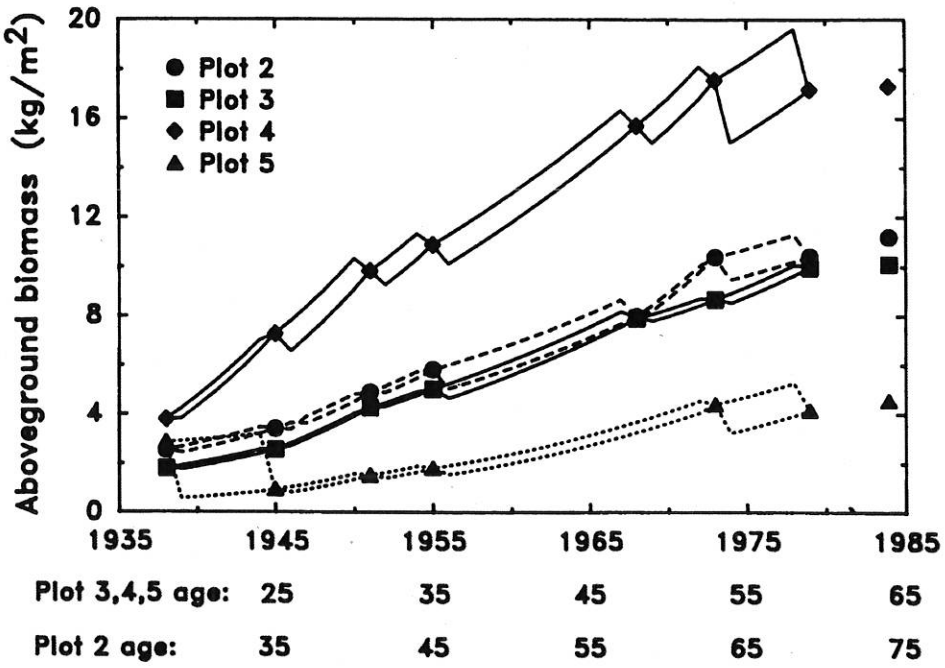

Figure 1. Total standing crop (aboveground dry biomass) on the plots from 1938 to 1984. The lines show the effects of using different assumptions about timing of mortality and recruitment between sample years. Trees were measured but not mapped in 1984, so biomass could not be estimated for 1980–1983. KEY: •Plot 2, ■Plot 3, ◆Plot 4, ▲Plot 5.

results for species, below), but then increased until 1973, reaching a value about five times the biomass in 1945. The other plots had fairly steady increases in standing crop from 1938 until 1973; all three reached values about five times their biomass in 1938. Since 1973, biomass on all four plots has been nearly constant. The small size of the plots makes conclusions difficult to draw, since the death of a single large tree can noticeably affect stand biomass, but the similarity among plots suggests that the plots have indeed reached a real plateau in biomass.

The different lines for each plot in Fig. 1 show the effect of different assumptions about the time of mortality and recruitment in each sample interval; the lines delimit upper and lower limits for biomass in each interval. The greatest uncertainty in biomass (i.e., the greatest difference between the upper and lower limits) occurred in plot 5 during the period 1939–1944 and in plots 2, 4, and 5 during the period 1974–1978; these were periods of higher mortality in the plots.

Since the approximate date of origin for the forest on each plot is known, the curves in Fig. 1 could be extrapolated back to zero, assuming that all the forests appeared after fires had more or less completely removed

vegetation on the sites. The greatest uncertainty in such extrapolation is in how fast each site was recolonized; depending on whether the new forests developed primarily from sprouts from extant root systems or from seeds, there could be considerable differences in the initial rate of biomass accumulation on each site. Clumping of maple and aspen stems on the plots suggests that most stems are probably of sprout origin, although patchiness of microenvironments and seedbeds after fire conceivably could have produced similar clumps of stems from seeds.

Bigtooth aspen was the dominant species, in terms of biomass, in 1938 on all plots except plot 5; it became the dominant species on plot 5 in the 1940s (Table 2). Bigtooth aspen has since maintained its dominance on all sites, with steady increases in biomass until the 1970s, although from 1955 to 1984 its percentage of the total biomass declined on plots 2, 3, and 4. Since 1938, there have been gradual increases in biomass of red pine, white pine, red oak, and red maple due both to growth of existing trees and to recruitment of additional stems (Table 2). The only major species with net declines in both absolute and percentage biomass from 1938 to 1984 were paper birch on plot 2 and trembling aspen on plot 5, although white pine on plot 3 experienced a small decrease in its percentage of the total biomass (Table 2). Only on plot 5 did dominance shift among species, from trembling aspen to bigtooth aspen. Trembling aspen had the greatest standing crop on plot 5 in 1938, but declined drastically by 1945. Sylvester (1939, unpublished University of Michigan Biological Station student paper) noted an insect infestation in 1939 that was killing trembling aspen but not bigtooth aspen on plot 5. However, the plot data also show declines in bigtooth aspen and paper birch between 1938 and 1945, perhaps due to a storm in 1940 (Sakai & Sulak 1985). Since 1945, trembling aspen has maintained a fairly constant total standing crop, while bigtooth aspen, paper birch, and red maple have increased their standing crops.

One example of the distribution of biomass among plant parts, for plot 4, is shown in Table 3. Boles (trunks) always accounted for the greatest fraction of the total standing crop, and the fraction increased from 1938 to the 1970s. Total bole biomass in 1979 was five times that in 1938. Live branches were the second largest component of the total standing crop; branch biomass in 1979 was 1.7 times that in 1938, although branches as a fraction of total standing crop decreased over time. The biomass of leaves increased by only 40% from 1938 to 1979, while biomass of dead branches increased only by a factor of 2, so that their relative fractions of total standing crop decreased. The small increase in leaf biomass resulted from a nearly constant aspen leaf biomass and small increases in leaf biomass of other species. Thus, the aspen-dominated canopy on this site apparently was nearly fully developed within a few years after the origin of the forest; due to the shade intolerance of aspen, once a maximum density and depth of the canopy was reached, no more aspen leaves could be supported regardless of the size of the boles. Additional leaves thus have been produced only by more shade-tolerant species. On the other plots, leaf biomass has also been relatively constant (data not shown), but at levels below that

TABLE 2: Aboveground biomass of each species on the plots, as a percentage of the total aboveground standing crop on a plot. Values are given for three sample years, to illustrate the general pattern seen over the entire sequence of sample years.

Species	Year	Plot 2	Plot 3	Plot 4	Plot 5
Bigtooth aspen	1938	79.0	39.3	85.4	10.9
	1955	76.4	48.6	86.2	29.3
	1984	61.9	43.2	82.3	44.1
Trembling aspen	1938	0.7	0	0.2	65.2
	1955	0.7	0	0	16.5
	1984	0	0	0	8.3
Red maple	1938	4.3	3.6	8.3	0.01
	1955	4.9	4.1	10.5	6.2
	1984	7.8	6.5	12.1	18.9
Red oak	1938	10.1	2.2	0	0
	1955	12.0	2.5	0	0
	1984	15.9	5.7	0	0
Paper birch	1938	1.8	5.4	0	22.5
	1955	2.3	2.7	0	43.7
	1984	0.3	3.1	0	25.4
Red pine	1938	0.7	38.4	0	0
	1955	2.2	33.7	0	0
	1984	9.9	31.8	0	0
White pine	1938	0.2	11.1	0	0
	1955	1.0	8.5	0	0
	1984	3.8	8.9	0	0.5
Sugar maple	1938	0	0	0.6	0
	1955	0	0	1.4	0
	1984	0	0	2.3	0
Beech	1938	0.03	0	0.1	0
	1955	0.1	0	0.7	0
	1984	0.02	0	1.2	0
Miscellaneous	1938	3.3	0.03	5.5	1.4
	1955	0.6	0.1	1.2	4.3
	1984	0.24	0.9	2.2	2.9

on plot 4; leaf biomass on these plots is possibly limited by nutrients rather than light.

Total yearly production generally increased from 1939 to 1979 on plots 2, 3, and 5, whereas production on plot 4 did not show such a long-term trend (Table 4). Production on plots 2 and 4 was highest in 1969–1973. It is not clear whether these peaks were temporary deviations from long-term patterns of gradual increase in production or whether there has been a real change in the trend since 1973. A decline in production on older sites is predicted by the regressions of site age versus production developed by Cooper (1981) for similar sites, but peak levels of production were several times higher than those predicted by Cooper's equations and the two plots are of different ages. In contrast, plot 3 has exhibited no drop in production levels since 1973 even though it has a composition and standing crop similar to plot 2 (Table 4). Plot 5 had by far the lowest yearly production, whereas

TABLE 3: Biomass of plant parts on plot 4 for the sample years. Mass values are kg/m^2. Percent values are percentage of total biomass in that year.

Year	Leaves		Live Branches		Dead Branches		Boles	
	mass	%	mass	%	mass	%	mass	%
1938	0.237	6.3	0.499	13.2	0.109	2.9	2.945	77.7
1945	0.307	4.2	0.792	10.9	0.145	2.0	5.435	74.8
1951	0.311	3.2	0.937	9.6	0.150	1.5	8.415	85.7
1955	0.305	2.8	0.976	9.0	0.153	1.4	9.442	86.8
1968	0.350	2.2	1.274	8.1	0.199	1.3	13.883	88.4
1973	0.371	2.1	1.418	8.1	0.222	1.3	15.553	88.6
1979	0.330	1.9	1.330	7.8	0.219	1.3	15.273	89.1

production on plot 4 was much higher than on any of the other sites (Table 4). The production on plot 4 for the years 1974–1979 (762 g m^{-2} yr^{-1}) compares favorably with that (617 g m^{-2} yr^{-1}) calculated by us for a plot established by Wells (1978), which is similar in site quality and forest age to plot 4. The Wells plot is roughly 25 times larger and should yield a more reliable estimate.

The two different assumptions about patterns of mortality and recruitment resulted in average production values for each interval that typically differed from the mean of the two values by less than 3%. Only in plot 5 in the 1939–1945 interval was there a large (30%) difference from the mean.

One example of yearly production by plant part, for plot 4, is shown in Table 5. Production of boles (trunk wood and bark) was roughly double the production of leaves, whereas production of branches was much lower. Production of each plant part as a percentage of total production was relatively constant over time (Table 5).

DISCUSSION

The reliability of estimates of standing crop and production produced via use of allometric equations necessarily depends heavily on the reliability of the equations used. Except for large red pine and white pine, our equations were derived from trees at the Biological Station, which decreases the errors that occur when equations derived from one site are applied to stands at another location. However, it is unknown how much error is involved in applying a set of equations derived over a relatively short period in the life of a stand to the development of the stand over time, i.e., how much the allometric relationship changes over time with changes in tree age, size, and density. A third limitation in using allometric equations typically occurs when rates of mortality and recruitment must be estimated. Here, overall rates of mortality and recruitment were known because individual stems were tracked; only the timing of mortality and recruitment between sample years was unknown. However, uncertainty in the date of appearance and

TABLE 4: Mean total yearly production on each plot for the intervals between sample years. Values are the average, over all years in the interval, of the calculated maximum and minimum values for each year, where maximum and minimum values were derived from different hypothetical patterns of mortality and recruitment. Units are g m^{-2} yr^{-1}.

Years	Plot 2	Plot 3	Plot 4	Plot 5
1939–45	285	307	807	131
1946–51	453	528	919	181
1952–55	491	497	815	183
1956–68	483	593	780	245*
1969–73	836	593	970	245*
1974–79	534	692	762	284

*mean for 1956–1973

date of death for stems appearing and disappearing between sample dates had relatively little effect on calculated standing crop and production for most of the study period, as demonstrated by the limits established by choosing extreme values. Early in the study, only plot 5, with considerable mortality between 1938 and 1945, exhibited a wide range of potential values between the sample years. Variation in the other plots was low because of low recruitment and low mortality of larger stems in these relatively young, aspen-dominated stands. Not until the 1970s, when some older, larger stems died, did plots 2, 4, and 5 also have the potential for much variability. Even so, such variation in estimation of both standing crop and production is necessarily less than that which occurs when overall rates of recruitment and mortality must be estimated, as is the case when individual stems are not tracked over time. For example, if mortality is not accounted for at all, estimates of production based solely on successive estimates of standing crop may be substantially lower than the "true" production. This occurs because the production estimate is low by a value equal to the standing crop of trees that died during the interval; any production by such trees before they died also will be missed.

Aspen is widely recognized to be a short-lived tree, often reaching ages of only 50 to 80 years, although some stems live well beyond 80 years (Fowells 1965). Thus, in the 1970s and 1980s, many of the original aspen stems on the plots have neared the end of their expected lifespans. Even so, no widescale death of aspen has yet occurred; several large trees died in the 1973–1979 interval, but there was little or no mortality between 1979 and 1984 (as estimated from comparisons of diameter distributions in 1979 and 1984). Sakai et al. (1985) studied a plot established in 1974 by Wells (1978) on a site close to and similar in quality to our plot 4 and also found very little mortality over the years 1974 to 1981. Aspen typically lives longer on sites of better quality (Kittredge 1938); one would therefore expect plot 4 to be the last plot to show deterioration of aspen.

Low or zero recruitment of aspen stems on the plots (Roberts & Richardson 1985) suggests that the composition of the forests will change

TABLE 5: Mean total yearly production of plant parts on plot 4 for intervals between sample years. Values are the average, over all years in the interval, of the calculated maximum and minimum values for each year, where maximum and minimum values were derived from different hypothetical patterns of mortality and recruitment. Mass values are g m^{-2} yr^{-1}. Percent values are percentage of total production in that year.

Years	Leaves		Live Branches		Dead Branches		Boles	
	mass	%	mass	%	mass	%	mass	%
1939-45	267	33.1	51.7	6.4	7.9	1.0	481	59.6
1946-51	271	32.7	51.4	5.6	6.8	0.7	560	60.9
1952-55	288	37.2	39.5	4.9	6.0	0.7	467	57.3
1956-68	305	41.8	32.7	4.2	5.2	0.7	416	53.4
1969-73	360	37.1	48.5	5.0	7.5	0.8	554	57.1
1974-79	347	45.5	24.4	3.2	4.7	0.6	412	54.1

considerably in the future. Although new aspen sprouts could appear after the old aspens die and create openings in the canopy, it seems more likely that the existing hardwood and pine stems will fill in the gaps. Thus, forests of pines, maples, and red oak will probably replace the present aspen-dominated stands, although clearcutting or other large-scale disturbances could promote regeneration of aspen.

Aboveground standing crop for temperate deciduous forests of the Great Lakes region has been estimated to range from 6 to 60 kg/m^2 (Crow 1978). Our plots are at the lower end of this range, but have standing crops similar to other aspen-dominated forests in the region. Crow (1978) found a value of 9.2 kg/m^2 for an aspen forest in northern Wisconsin, similar to plots 2 and 3. Bray and Dudkiewicz (1963) and Pastor and Bockheim (1981) found values of 20.7 and 19.7 kg/m^2, respectively, similar to plot 4. Relatively cool temperatures and a short growing season at the northern edge of the temperate forest zone plus sandy soils low in nutrients and water-holding capacity are likely major contributors to the low standing crops at the Biological Station. Differences between the plots strongly suggest that soil fertility is a major limitation on growth on many sites; soil fertility was the major environmental difference between plot 4 and the other plots (Roberts & Richardson 1985). Moreover, the Biological Station forests presently are dominated by an early successional species and have not reached a stable state. With time, successional processes may produce a forest with more biomass on these sites, as bigtooth aspen is replaced by longer-lived, heavier-wooded hardwood and pine species. However, there may also occur a countering decrease in biomass due to a change from an even-aged aspen forest to an uneven-aged, mixed forest with gaps due to mortality.

Total net production in temperate forests has been estimated at 0.6 to 3 kg m^{-2} yr^{-1} (Westlake 1963). Our estimates for aboveground production are compatible with these and indicate that our stands are at the low end of the range for temperate forests as a whole. Certainly, cool temperatures and

sandy soils again contribute to these relatively low values. Stand age is probably not a major factor; Cooper (1981) predicted peak production in aspen stands at around 45 years. Our stands had maximum production values in the 1970s, at stand ages of 50–70 years. The relatively constant, higher production on plot 4 apparently is due to the denser, more uniform stand on that more fertile site. However, we cannot discount the possibility that some of the variation among plots is due to genetic differences among aspen clones or even partly due to errors in applying one set of allometric equations to trees on sites of different fertility. On plots 2, 3 and 5, production has increased with time, presumably as the canopies filled in the original gaps in the lower-density, patchy stands on these lower-fertility sites. Even so, production on these three plots may now be leveling off, as the older aspen stems near the ends of their expected lifespans.

SUMMARY

Aboveground biomass and production were calculated for forest stands on four 0.1 acre (0.04 ha) permanent plots in northern lower Michigan, U.S.A., on which individual trees were measured at 4–13 year intervals from 1938 to 1984. Stands were 19–29 years old in 1938. Bigtooth aspen (*Populus grandidentata* Michx.) was the dominant species, in terms of biomass, on three of the plots for the entire period; it was the dominant species on the fourth plot after 1960. Standing crop biomass increased five-fold from 1938 to 1984 on three of the plots; biomass on the fourth plot declined until 1945 due to mortality of stems from unknown causes but then also increased five-fold by 1984. The rate of increase in standing crop has slowed since 1973. In 1984, standing crop was 17.5 kg/m^2 on a higher-fertility site and ranged from 4.8 to 11.2 kg/m^2 on the three lower-fertility sites. Total yearly production doubled from 1938 to 1979 on the three lower-fertility sites, reaching values of 284 to 692 g m^{-2} yr^{-1} in 1979. Production on the higher-fertility site varied from 780 to 970 g m^{-2} yr^{-1}, with no significant trend when viewed over the entire period. Uncertainty as to time of appearance or death of stems between sample dates was demonstrated to have relatively little effect on calculated standing crop and production.

ACKNOWLEDGMENTS

We thank Robert Vande Kopple and Martha Samson for assistance with the plot data. We thank all those persons, many of them unknown to us, who participated in measuring the plots over the half-century since their establishment. Supported by the United States Department of Energy under contract DE-ACO2-79EV10091.

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